CONTRIBUTIONS TO THE LIFE-HISTORIES OF PLANTS. NO. V.

BY THOMAS MEEHAN.

On the Anthers of Lappa major.

I have placed on record that the column of anthers of many composites, maturing before the style has finished its growth, is drawn up out of the floret until resistance is weak enough to allow the stigmas to escape from the staminal tube. As in almost every behavior of plants, there are extremes here as well. In some species the style easily escapes from the staminal tube, and the stamens are drawn but little, if any, above the mouth of the floret; in others the stamens are drawn to a considerable length before, they are drawn back to their normal position, by the elasticity of the filaments. In *Lappa* the other extreme is reached. The tube is drawn so far beyond the floret, that the caudate bases of the anthers are past the mouth of the corolla, and cannot get back again. The staminal tube, therefore, presents a condition unusual in composite flowers.

The Pollination of Crucianella stylosa.

In the Proceedings of the Academy of Natural Sciences, 1887, p. 325, I noted that the elongating styles of *Cephalanthus occidentalis* forced the clavate stigma through the four anthers, clearing out almost completely the pollen from the anther sacs and carrying up the densely pollen-covered stigma to its ultimate full growth, ensuring the most perfect self-fertilization. I also showed that the elongation of the style and full growth of the pistil were very rapid, commencing about 8 P. M. and reaching their full length in about half an hour.

Observing the past summer that another Rubiaceous plant, allied to *Galium* or *Asperula*, *Crucianella stylosa*, Trin., a native of Persia but growing in my garden, had long exserted styles, similar to *Cephalanthus*, I was moved to cut some branches and place them in water for study as in the former case.

We have here five stamens, instead of four, and the large stigma is forced through the center, just as in the manner described in *Cephalanthus*, evidently pushing up against the closed 5–parted limb of the corolla, which then expands, the style with the pollen-covered stigma continuing to its full growth. As in the case of the *Cephalanthus*, the pollen is so nearly cleaned out of the anthers by the up-

ward growth of the stigma, that scarcely any is left in the anther cell, and yet so delicately is it done, that the five lines of pollen, as cleaned out from the five anthers, are generally discernible. Nature could not have made a better arrangement for making cross-fertilization impossible.

All attempts to ascertain the precise time of the opening and elongation of the style failed. Though I made several successive attempts with fresh flowers, none opened up to 11 P. M., unless touched with the point of a pin, when the limb would part with an elastic sort of spring, becoming expanded so instantaneously as to defy the eye to detect the motion. In the morning, two or three hours after sunrise, the room, however, being "pitch dark" from shutters, a number of newly opened flowers, with their pollen-covered stigmas would be found, but not with the styles much exserted. The elongation seemed to be done gradually through the day, not reaching full length till night-fall.

Note on Unisexuality in Connection with the Order of Flowering in Willows.

After the flower buds have been formed and in many species of plants have reached a certain size, they remain at rest until the axis has reached its full growth, when this has been accomplished the flower buds resume activity. In the well known case of *Liatris*, and indeed in most allied genera of Compositæ, the renewed development of these flower buds is from the apex downwards. In other cases, some Fumariaceæ for instance, the lowest bud on the spike or raceme starts the renewal. In most willows the renewal of growth is from the middle of the branch. If, for instance, there may be eleven catkins to be produced from as many axils along the stem, No. 6 will be the first to expand, 5 and 7 next, then 4 and 8, 3 and 9, 2 and 10, and finally 1 and 11. Singularly enough, this order does not extend to the catkins themselves. In them the growth ceases as soon as the anthers reach their full size, and the stamen remains at rest until the axis of the catkin has reached its final length. Then the filaments are formed and the perfect stamen assumes its full proportion but gradually from the apex downward.

It seems to me still more evident that, as I have already pointed out,[1] this arrest of growth at a certain period and subsequent resump-

[1] Proc. Acad. Nat. Sci., Phila., 1883, p. 85; 1884, p. 117; 1885, p. 117.

tion furnishes the clue to the law governing that abortion in flowers which renders the hermaphrodite unisexual. In the maple, as in the case referred to, there is a rest when the anther and pistil reach a certain point. When growth is again resumed, the filament is produced and the stamen elongates, while the pistil remains dormant. Then we have fully developed male flowers. In another case growth is resumed only by the gynœcium, the fully formed anthers remaining sessile and barren at the base. Then we have the female flowers in the maple tree. This arrest and resumption of growth in the parts of flowers was noted by the author many years ago in the flowers of the Compass Plant, *Silphium laciniatum.*[1]

The facts here noted in connection with the willow refer to the male aments.

On the Varying Character of Dichogamy in Flowers of Corylus Avellana.

In several papers, in recent years, I have noted that dichogamy is not a fixed character in plants, brought about by any relation between insects and flowers, but is affected by climate and season. A species proterandrous under one set of circumstances, will be proterogynous under another. I have also shown that certain conditions of temperature will affect the female flowers or female organs of hermaphrodite flowers when the male organs will remain quiescent, and that other conditions will advance the male organs rapidly, while the female organs remain at rest.

My observations on the hazel nut, *Corylus Avellana*, for several years past have shown remarkable variations. A few very warm days in cold winters will bring the male flowers to perfection two months before the female flowers open, dying away so completely as not to leave any for fertilization, so that the plants would be wholly barren for that season. Occasionally the openings of the male and female flowers have been nearly simultaneous, when a good crop of nuts from complete fertilization has resulted.

This season is the first since the observations have been undertaken when the results have been reversed. The female flowers are now (Jan. 11th, 1890) abundantly in bloom, while the catkins are far from mature. In former years the flowers have always been proterandrous—this season they are proterogynous.

Although the deductions I have heretofore made—that male flowers, or male organs of flowers, mature rapidly under a com-

[1] Ibid, 1870, p. 117.

paratively high temperature, while the female organs continue quiescent, scarcely needed further confirmation, the present additional point that under a prolonged moderate temperature the female will advance more than the male has not been brought out so well before. This, in the hazel-nut or filbert, has never been noted in America heretofore to the best of my belief. So unexpected was the fact as to make a statement in the Transactions of the Royal Horticultural Society of London, vol. V, 1824, p. 311, appear almost incredible to one not familiar with such observations as I have recorded. The Rev. Geo. Swayne says at the page quoted "casually passing by them (the trees) in the second week in February, 1820, I was rather surprised to see a considerable number of scarlet blossoms thereon in a state of expansion, but at the same time very few catkins, and those few seemed to be in a very imperfect state, not a single one being prepared to discharge its farina." Here we have a precisely similar observation in these Philadelphia plants, only four weeks earlier than Mr. Swayne saw them.

The season has been one of the most remarkable known for many years. Instead of the thermometer varying from the the freezing point to zero, with occasional spells of a day or two between at 50° or 60°, the thermometer has only once fallen just beneath the freezing point, while at no time has it risen above 50°. The general remark with English people is that it is an open English winter. The English hazel, therefore, finds itself pretty much at home, and has fallen back on its natural habit, as we may suppose, of producing both sexes nearly simultaneously.

The deductions from former observations may again be repeated:—

Under sudden high temperature the male flowers of the hazel will open and perfect, long before the female flowers are affected by the same temperature.

Under long continued temperate heat, the female flowers will advance more rapidly than the male.

There is no specific rule in dichogamous plants. A plant with flowers proterandrous in one season or one country, may be proterogynous in another.

My former observations were made on various flowers, though confined to the hazel in this paper.

Dioecism in Labiatæ.

In some observations recorded last year I noted that the sexual disturbances observed in some European Labiatæ, did not seem to

extend to distinctively American species, though Old-World species retained the peculiarities when translated here. I now find in *Pycnanthemum* similar conditions. *P. lanceolatum* Pursh, a large clump of which from one original plant growing in my garden produces flowers apparently perfect, wholly fails to perfect seed. Close beside it is a clump of *P. muticum* Pers. with no trace of stamens, but with an exserted and in every way perfect pistil, seeding abundantly. On close examination it is evident that the pistil in the former is not as perfect as it appears to be. It is never exserted, nor do the stigmatic lobes perfectly expand. There is no doubt that these plants practically represent staminate and pistillate plants respectively.

The abundant seeding of *P. muticum* under the above detailed circumstances, could only result from the abundant pollen of *P. lanceolatum*, and the seeds produced by the former must of necessity produce hybrid plants.

Prof. Gray notices in Synoptical Flora a number of variations near *P. muticum*, and of one, *P. leptodon*, remarks "perhaps a hybrid between *P. muticum* var. *pilosum*, and *P. Tullia* var. *dubium*." The observations here recorded add greater probability to the suggestion of the hybrid origin of intermediate forms in this genus, by pointing out the exact method under which hybridism is brought about.

It may be repeated here that, as noted by the author long since, cross-fertilization must be regarded as the hand-maid of heredity, rather than as a factor in the evolution of form. Its duty is to bring nearer home that which has wandered.

Self-Fertilizing Flowers.

A large number of flowers are so arranged as to render self-fertilization difficult, and in many cases impossible. Numerous observers have placed on record what they have discovered in the line of these facts, and have rendered inestimable service to science. There may be a question whether the interpretation of such facts be legitimate; there can be no question as to the value of the facts themselves.

Observations on the other side have not been as numerous, yet they seem no less interesting. The number that are not only adapted to self-fertilization, but actually self-fertilized, seems as large as that of the other class. We may leave the interpretation till the record is more complete.

There is one salient point in connection with the whole subject worth placing prominently before the student, and which will be found sustained by the most superficial examination, namely: All plants that are arranged for self-pollination are abundantly fertile, and have a great advantage of numbers in the struggle for life, while those that have to depend on external agencies are usually much less productive, and even though the progeny may be found to have greater vegetative vigor, or some other element of strength. The influence of numbers is certainly with those which self-fertilize. If Providence is on the side of the strongest battalions, the argument of nature is on the side of self-fertilization.

It has come to be a rule with the author of this paper, whenever any plant is unanimously productive, to look for and to find arrangements for self-fertilization. A few instances of more than usual interest, drawn from last summer's experience, are herewith offered.

Trichostema dichotomum.—This pretty blue flowered Labiate is well known as "Blue Curls," and is common in sandy places along the Atlantic Sea-board. In many Labiates the lips of the cloven stigma remain closed till after protrusion from the flower. Such cases are commonly with those that are classed as arranged for cross-fertilization. In many, however, the lips expand before the flowers are open and receive pollen from their own anthers, which mature simultaneously. In this plant this is the case, and the inner face of the stigma lobes are so bent that they come in close contact with the anthers from the curved up filaments and finally emerge from the flower, as it expands, covered with own-pollen.

Buddleia curviflora.—Noting that this pretty Japan shrub was enormously fertile, evidences of self-fertilization were at once looked for. The narrow tube of the flower is nearly an inch long, the anthers being inserted about the middle, or at half an inch. The ovarium with the pistil occupies about a quarter of an inch. The half inch above the anthers is densely clothed with stiff hair, completely closing the narrow tube. The brush would effectually cleanse an entering proboscis of foreign pollen, or a withdrawing one of the flower's own pollen. But it is not necessary to speculate on what an insect could or might do, for the anthers burst before the flowers open, and cover the whole stigma with abundant pollen. No one examining these flowers can fail to be convinced that they are ingeniously arranged for self-fertilization. As in all cases of flowers with tubular corollas, the humble bees in this region rifle the flower

of its sweets by boring the base of the corolla tube. *Buddleia Lindleyana* exhibits similar characters.

Vitex Agnus-castus.—This Verbenaceous plant from the south of Europe common in gardens as the "chaste tree," is abundantly fertile. The anthers burst their pollen sometimes as much as twenty-four hours before the flowers open. The pistil is cloven as in many Labiates, but is remarkable for having the lips expanded at a very early stage. The pollen as it escapes from the cells, falls on the stigmatic surfaces. The stigma at this time may be regarded as functionless; but the pollen remains attached, and is borne up as the style elongates and performs its part in the economy of plant life at once when the flower expands. After expansion the pistil curves upward. The flowers seem great favorites with insects, especially with Lepidoptera. Repeated observations failed to note a single case where a stigma was touched by a visiting insect. Humble-bees bore through the tube for their share of the nectar.

Hypericum mutilum.—This weed, common in damp ground, is abundantly fertile. An examination of an unopened flower, shows the anthers to be entangled among the styles from which on expansion of the flower, the weak hair-like filaments are unable to extricate them. The anthers mostly remain in this position, shedding their pollen over the stigmas, getting in their early work to the exclusion of intruding pollen. *H. Canadense* behaves in a similar manner.

Phytolacca decandra.—Assured, from its abundant fertility, that the common "Poke-weed," was adapted to self-fertilization, I was led to examine a flower, and found that it was fertilized before opening. The stamens are curved over, completely covering the gynœcium, and the anthers discharge the pollen in great profusion over the styles. These have their stigmas partially decayed before the flowers open, showing that their functions have been wholly concluded while the flower was unexpanded.

Lycopersicum esculentum. Noting that the common Tomato, and its neighboring Solanaceous plant, *Capsicum grossum*, the Bell-pepper of gardens, had nearly or quite every flower fertile, an examination of a few flowers late in the season, showed plainly that they are arranged to insure self-fertilization. The anthers of the Tomato are connate, and drawn together in a cone over the pistil. The anther-cells burst simultaneously with the expansion of the corolla, and the discharged pollen covers the stigmatic apex. It is impossible for the flower, under any ordinary circumstances, to receive

foreign pollen. The large purple anthers of the Capsicum are drawn closely together and discharge pollen copiously over the stigma.

Lycopus Virginicus L.—It cannot be said that there is any arrangement of the parts of the flower suggestive of special adaptation to self-pollination, but the later flowers of the season, borne on the stolons, are often pushed into the earth in the bud and expand wholly beneath the surface, producing seeds as abundantly as those on the erect stems. No one will doubt, on carefully observing the plants that the flowers self-fertilize. Dr. Gray seems to limit the tuberiferous character of this species to a depauperate form growing from Lake Superior northwards. The tubers are freely borne by the typical form around Philadelphia, and they are often as large as Kidney Beans.

Hamamelis Virginiana L.—The arrangements for self-pollination here are among the most interesting known to me. It is well-known that the anther-cell opens by an operculate lid or valve. What might be termed the hinge to this lid is on the upper part of the stamen. When ready to expose the pollen, the lid previously pointing downward, becomes perfectly erect. The face which, previous to opening, faced one point of the horizon, is turned to the opposite, and the inside face becomes the outside. The pollen adheres to the inside face of the valve, and so complete is this adherence, that on the erection of the valve, every part of the pollen is withdrawn from the cell. The erection of this valve is, however, accomplished instantaneously, and the sudden jerk dislodges some of the pollen, which is scattered around. Some falls back into the cell, some over the adjacent stigmas, but a large portion still adheres to the face of the lid, falling away gradually as moved by the wind or other agency.

It may be well to note here the order in which the parts of the flower successively mature. As the four strap-like petals expand, neither anthers nor stigmas have reached maturity, which seems to be the work of the second day. As the stigmas become viscid, a pair of anthers only expose the pollen. One anther, and one cell only of each anther, bursts at a time, the other follows some time during the same day. Before evening of that day, the four cells expose the inner pollen-clothed surface of the lid. The pair of stamens that open first are those that are in front of the pair of styles—that is, the pair which alternates with them. The next day the pair on

a line with the pair of styles go through the same process. It is customary to describe the stamens and petals of *Hamamelis* as in fours. These observations show them to be really in pairs.

The *Hamamelis* flowers in autumn when the leaves are falling. These observations were made between the 15th of October and 1st of November. The insect world has not wholly gone to its winter rest, but it is a very dull and inactive world. I see no insects at work on the flowers,—but I may be told this is an observation easy to be made on any plant. Such a remark has been made on one of my former recorded observations. One who has growing plants within a few score feet of his library, who has watched them many times a day, and many days during a couple of weeks, might almost venture to say no insects visited them, but accurate statement could only record that no insects were noted visiting the flowers. In the same spirit it is but fair to say that the author has not actually seen the valve of the anther fly up suddenly as described above. He has watched with a lens in hand assiduously for the pleasure of seeing one, without success. He has, however, seen them erect, where but a few seconds before they were closed, warranting him, as he believes, in assuming the fact as recorded.

On the Male and Hermaphrodite Flowers of Æsculus parviflora.

The enormous number of flowers in proportion to fruit produced in *Æsculus parviflora* Walt. may have attracted attention. It is recorded as being "polygamous." The flowers seem to be either perfect or male.

It seemed of some interest to carefully note the behavior of one I had the opportunity to examine several times daily. The plant is of some age, and forms a bush thirty-six feet in circumference. Counting over a few square feet and multiplying by the whole area, I estimated one thousand spikes of flowers. An average spike gave four hundred flowers, so that the total would be 400,000 on the plant. About one half of these had not a single perfect flower,—and the greatest number counted on any spike was forty-six. This would give an average of twenty-three to five hundred spikes or 12,500 hermaphrodite or perfect flowers as against 387,500 male flowers.

In the animal kingdom the number of males born to female is about equal. In the monoecious or dioecious plants it must have been noted that great disproportion exists, but one so great was unexpected.

In all cases where the branches of the previous year had matured in partial shade, the flowers on the spike proceeding therefrom were wholly male. This is in accord with the views heretofore developed by me that conditions unfavorable to perfect nutrition are unfavorable to the development of female flowers. In the branches that had been developed under conditions favorable to nutrition, some would have spikes less vigorous than others, but so far as I could see, this had no effect on the production of the sexes. As many perfect flowers would be found on a comparatively weak as on a strong spike.

What I have placed on record in relation to growth-rhythms in *Acer dasycarpum*, *Acer rubrum* and some other plants, occurs in these flower buds also. At an early stage in the bud, the anthers are fully formed and the gynœcium reaches a certain stage, when a resting time occurs. When growth is renewed the ovary with its pistil proceeds to move forward rapidly, while the filaments proceed slowly; or the latter move rapidly and the gynœcium continues wholly at rest. In the former case we have the perfect, in the latter the male only or barren one.

It is evident that up to the time when this last growth-rhythm begins, the flower may be male or female (hermaphrodite in this case.) It is male or female simply as the renewed growth-force is directed towards the gynœcium, or to the stamens alone.

The development of the stamens presents points of interest. In the hermaphrodite flower, the point of the stigma and points of the anthers appear simultaneously bursting through the petals, then rest for some twenty-four hours. The growth of these parts is then very rapid, the stamens and pistils extending to nearly an inch beyond the calyx. This renewed growth commences soon after sun-rise, and ceases with sun-down. The anthers do not burst their cells on the day this growth is in progress. The following day, however, one anther sheds its pollen, the next day another, the third day another and on the fourth day all the remaining burst nearly simultaneously.

It has become the habit in observations of this kind, to suspect that the whole behavior has some relation to the visits of insects, and to cross-fertilization. But though endeavoring to trace such a relation here, it could not be ascertained. If the division of the sexes is with a view to economy in energy, the enormous disproportion of male to female flowers strikes the thought unfavorably. If we watch the flowers closely we find bees and other insects visiting them

in great numbers during the day, and numerous Lepidoptera by night. But none seem to be pollen gatherers; they collect nectar only so far as we can see. The stigma and anthers extended so far from the mouth of the corolla, are never touched by any insect and receive no insect aid whatever in pollination. The two earliest developing anthers are almost in contact with the stigma, which is at least quite as likely to receive pollen from them as from the other flower. Granting, however, that pollen may come from other contiguous flowers and reach the pistil before its own pollen has had the chance, it is physiologically of the same character, and could scarcely be considered as coming within the scope of cross-fertilization.

To my mind no deductions of economic value to the plant can be drawn from these observations.

On the Direction of the Spiral Twist in the Leaves of the Norway Spruce.

The true leaves of Pines are adnate, or perhaps more properly speaking, connate with the branches. Occasionally the apex is free as a mere membranous scale; or when the branch is young, or under circumstances not well understood, but evidently influenced by various phases of nutrition, instead of a mere scale, a regular green leaf, often articulated, is produced from the free apex. When the axial growth is arrested, the green leaves, having nothing to grow to, develop as ordinary leaves would do, and then we have the fascicles of Pine needles, or the verticils of leaves as in the Larch. The pine "needles," spring from a spur as do the leaves of the Larch, only that in the former the arrested woody axis is beneath the outer bark and invisible.

In the Norway Spruce, *Picea excelsa*, the adherent leaves are arranged around the branches from left to right as we look at them, or, as some would say, in a direction contrary to the sun. The free portion—that above the articulation—remains strictly erect, as a general thing, so far as the central or leading shoot is concerned. When the axial growth terminates, the membranous leaves having no axis to adhere to, usually form the bud scales, which are arranged as in miniature cones. We see that the cone of the Norway Spruce is but an arrested and metamorphosed branch, in which what might have been connate leaves, are now free and have become the bracts beneath the scales of the cone. These bud scales do not, however, always remain as scales, but develop to an articulation with a perfect green leaf, as in the regular growth along the stems just as in the

Larch or the regular Pine needles. Having no axis to adhere to, these true leaves in the Norway Spruce seem to grow the larger by reason of their freedom. In some cases these leaves from the bud scales are large enough to simulate those at the apex of *Sciadopitys*, and give the same parasol-like appearance to a spruce branch.

The chief point of this paper is to call attention to the direction of the spiral or twist of these free leaves. Along the central stem, as already noted, the free leaves are usually on a line parallel with that stem, but occasionally they twist to the right or to the left. The same is true of those of the buds. They nearly all twist one way or other. As the adult leaves around the stem all coil in one direction, one might reasonably expect the free leaves to do the same. It is surprising to find that they frequently do not, as many will be found on the same plant twisting in either direction, though every leaf in the same bud has the twist in the same direction.

Attempts have been made to explain the law underlying the spiral arrangement of the leaves of plants. The indifferent directions taken by the leaves of the Norway Spruce, as detailed, would indicate that, whatever that law may be, it is rather local than in control of the whole system governing the growth of the plant.